Spatial variation in invasive silver carp population ecology throughout the upper Mississippi River basin

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Spatial variation in invasive silver carp population ecology throughout the upper Mississippi River basin

Abstract
Understanding spatial variation in non-native fish species population ecology is imperative, where environmental, biotic and invasion-related mechanisms contribute to spatial heterogeneity. Established populations of invasive silver carp Hypophthalmichthys molitrix are currently found throughout a large portion of the upper Mississippi River (UMR) basin. Despite their recent invasion and broad environmental tolerances, silver carp population ecology and linkages to environmental conditions in the UMR remain understudied. There were two objectives for this investigation: (a) to estimate correlations among population characteristics and the influence of latitude and the time since first detection, and (b) to model the influence of river discharge and temperature on growth early in life to age 3. We estimated spatial variability in silver carp population characteristics and dynamics from nine sites across the UMR and assessed if biotic, abiotic or invasion-related (time since first detection) variables influence spatial patterns. Silver carp body weight, size structure, annual mortality, and growth parameters varied among locations. Silver carp recruitment was less stable for populations with higher relative abundance estimates and where carp were first detected ≥20 years ago whereas maximum carp age decreased with increasing latitude. Although model selection indicated silver carp length at age 3 was associated with mean daily discharge (m3/s) coefficient of variation, mean May–June temperatures, and ordinal date of maximum discharge, parameter coefficients and effect sizes were small and not biologically meaningful. Our results suggest that silver carp populations are governed by intraspecific mechanisms, but time-dependent changes in populations may partially underpin heterogeneity across populations. Our study helped further disentangle silver carp population ecology in the UMR by understanding carp ecology as a function of their invasion.

Keywords
growth, invasive species, Mississippi River, population dynamics, silver carp

Disciplines
Ecology and Evolutionary Biology | Natural Resources Management and Policy | Population Biology

Comments

Authors
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Abstract
Understanding spatial variation in non-native fish species population ecology is imperative, where environmental, biotic and invasion-related mechanisms contribute to spatial heterogeneity. Established populations of invasive silver carp *Hypophthalmichthys molitrix* are currently found throughout a large portion of the upper Mississippi River (UMR) basin. Despite their recent invasion and broad environmental tolerances, silver carp population ecology and linkages to environmental conditions in the UMR remain understudied. There were two objectives for this investigation: (a) to estimate correlations among population characteristics and the influence of latitude and the time since first detection, and (b) to model the influence of river discharge and temperature on growth early in life to age 3. We estimated spatial variability in silver carp population characteristics and dynamics from nine sites across the UMR and assessed if biotic, abiotic or invasion-related (time since first detection) variables influence spatial patterns. Silver carp body weight, size structure, annual mortality, and growth parameters varied among locations. Silver carp recruitment was less stable for populations with higher relative abundance estimates and where carp were first detected ≥20 years ago whereas maximum carp age decreased with increasing latitude. Although model selection indicated silver carp length at age 3 was associated with mean daily discharge (m³/s) coefficient of variation, mean May-June temperatures, and ordinal date of maximum discharge, parameter coefficients and effect sizes were small and not biologically meaningful. Our results suggest that silver carp populations are governed by intraspecific mechanisms, but time-dependent changes in populations may partially underpin heterogeneity across populations. Our study helped further disentangle silver carp population ecology in the UMR by understanding carp ecology as a function of their invasion.

**KEYWORDS**
growth, invasive species, Mississippi River, population dynamics, silver carp
Non-native fish species establishment is one of the main threats to the integrity and health of rivers across North America (Allen & Flecker, 1993). The ability to adapt to environmental conditions in novel ecosystems can determine whether or not a non-native species will establish (Sax & Brown, 2000; Shea & Chesson, 2002); however, environmental conditions fundamentally influence the growth and demographic rates of established non-native species populations (e.g., Weber et al., 2010; Wood & Budy, 2009). Thus, understanding patterns of variation and habitat-population linkages provides insights into processes that influence non-native species range expansion and distribution (Kolar & Lodge, 2001; Olden et al., 2006), temporal population trends (e.g., Fausch et al., 2001; Wood & Budy, 2009), and their potential effect on invaded ecosystems (e.g., David et al., 2017; Peterson et al., 2002; Sakai et al., 2001).

Establishment and invasion processes are often influenced by the interaction of abiotic and biotic factors, both operating at multiple spatial and temporal scales. In rivers where conditions are usually more dynamic than in lentic systems, habitat conditions (local and regional) can determine the extent to which a non-native species invades and subsequent population structure (e.g., Warnock & Rasmussen, 2013). Interrelationships among population-level biotic factors such as population density, condition, growth, recruitment and size structure can indicate which density-dependent factors, if any, that contribute to spatial variation in populations throughout an invasion or when established (e.g., Coulter, MacNamara, et al., 2018; Rose et al., 2001; Weber et al., 2010). Abiotic factors can also be important and are often associated with spatial variation in river fish populations. For non-native riverine fish species, connectivity among river reaches (e.g., Sakai et al., 2001), water temperature (e.g., Coulter, Tristano, et al., 2018; Kornis et al., 2013; Warnock & Rasmussen, 2013) and river discharge (e.g., Fausch et al., 2001; Wood & Budy, 2009) all play roles in determining the spatial variation of populations throughout an invasion and during critical life periods.

Invasion patterns undoubtedly rely heavily upon the population ecology and biotic and abiotic tolerances of a species (Dick et al., 2017; Kolar & Lodge, 2001; Ricciardi et al., 2011), but it is also important to consider information about invasion patterns (e.g., Brandner et al., 2013; Havel et al., 2015; Azzurro et al., 2016). In rivers where species movement is the most likely mode of range expansion, non-native fish will move into adjacent river reaches bidirectionally, but dams and other anthropogenic river modifications can delay or hinder fish movement (e.g., Coulter, Brey, et al., 2018; Tripp et al., 2014), causing invasions to be gradual. The timing of detection events can, therefore, describe the context of the invasion that can vary from site to site within and among rivers. Consequently, evaluating non-native species population ecology as a function of their invasion is important for further understanding spatial heterogeneity throughout invaded regions.

Non-native silver carp Hypophthalmichthys molitrix population abundance increased substantially throughout the Mississippi River basin from 1995 to 2015 (DeBoer et al., 2018; Iorns et al., 2007; Kolar et al., 2007). First documented in a Mississippi River tributary in east-central Arkansas during the mid-1970s (Freeze & Henderson, 1982), silver carp gradually moved into upstream river reaches and currently inhabit tributaries within 20 states (Nonindigenous Aquatic Species, 2020). In some areas throughout the Mississippi River basin, silver carp are highly abundant (up to 2,544 carp per river km [rkm]; Sass et al., 2009) and likely compose a majority of the fish assemblage biomass. Silver carp are planktivorous filter feeders (Kolar et al., 2007) and outcompete both juvenile and adult native fish for plankton resources at high densities (e.g., Iorns et al., 2007; Pendleton et al., 2017). Competition with native fish species is a particular concern in the Mississippi River where native species decline from anthropogenic modifications and activities is evident (e.g., Wiener et al., 1998) and silver carp may act in concert to further exacerbate population declines (Chick et al., 2020; Crimmins et al., 2015; Solomon et al., 2016). Silver carp are, therefore, considered an injurious fish species, and understanding their invasion and population ecology for improved population control is imperative (Conover & Simmonds, 2007).

Silver carp can migrate long distances (Calkins et al., 2012; Coulter et al., 2016; DeGrandchamp et al., 2008) and tolerate a wide range of river conditions (see Kolar et al., 2007), facilitating their broad distribution in the Mississippi River basin. Nonetheless, silver carp population ecology and linkages to environmental conditions remain understudied. Relationships between abiotic factors and silver carp reproduction and recruitment are well understood (e.g., elevated discharges increase reproduction and recruitment; Camacho et al., 2020; Coulter et al., 2016; Kolar et al., 2007; Larson et al., 2017; Sullivan et al., 2018), but few investigations into abiotic effects on established adult populations are undertaken (see Stuck et al., 2015; Coulter, MacNamara, et al., 2018). Silver carp population structure varies among river reaches throughout the Mississippi River basin, suggesting that differences in local conditions or invasion histories influence populations. Yet, regional variation in silver carp populations and the influence of biotic (e.g., density-dependent factors), abiotic (e.g., river discharge and temperature), or invasion-related mechanisms governing variation are not known and remains a significant knowledge gap in the ecology of invasive silver carp.

We examined biotic factors, river conditions, and invasion history associated with spatial variation in silver carp population ecology in the upper Mississippi River (UMR) and four major tributaries. Specifically, we used data from nine sites across the UMR to calculate a suite of silver carp population characteristics: relative abundance, body weight, growth (von Bertalanffy parameters and mean length at age 3), population size structure, annual mortality, and recruitment variability. Our first objective was to compare and determine the degree of correlation among silver carp population characteristics and to determine the degree that latitude and the time since first detection influence populations. Our second objective was to determine how metrics of river discharge and temperature influence silver carp length at age 3, a measure of growth early in life. We hypothesised that silver carp population characteristics are spatially structured,
where populations inhabiting sites where carp have been present longest and are more abundant would exhibit different population characteristics (e.g., Hayer et al., 2014). We also hypothesised that elevated discharges and temperatures during May-June (i.e., spawning period) would increase silver carp length at age 3 since juvenile carp use floodplain habitats (Kolar et al., 2007). Our results will help further disentangle silver carp population ecology throughout the UMR and the role that river conditions play in governing populations (e.g., Sullivan et al., 2018) to better explain the complexities driving the silver carp invasion.

2 | METHODS

2.1 | Study area

The Missouri, Des Moines, Illinois, and Wabash rivers are four major tributaries of the UMR where silver carp captures are commonplace, reproduction occurs, and recruitment is documented (i.e., established populations). As a result of human-driven modifications, the contemporary flow regimes of the Des Moines, Illinois, Missouri, and Mississippi rivers consist of an unnaturally pooled and regulated hydrograph upstream and a more natural hydrograph in downstream portions where floodplain habitats disperse floodwaters. In contrast, the Wabash River contains a single main stem dam near Huntington, Indiana where 661 rkm of free-flowing river is present upstream of the confluence with the Ohio River. Silver carp were first documented in rivers approximately 400 rkm downstream of the most southern extent of the study area (Freeze & Henderson, 1982). The progression of the silver carp invasion throughout the UMR from sighting or collection data indicates that the upstream expansion advanced gradually (Nonindigenous Aquatic Species, 2020), suggesting that the number of years that carp populations have occupied rivers varies throughout the basin. We excluded areas where silver carp were first detected within the last 10 years as populations may not be established yet. In all, the study rivers encompass a large diversity of environmental conditions and silver carp invasion histories that could influence carp populations (site-specific details are provided in Table 1).

2.2 | Field sampling and laboratory analysis

We collected silver carp from April through November 2015 at nine sites across the Mississippi, Missouri, Des Moines, Illinois, and Wabash rivers (Figure 1). Specific sites were selected based on the location of river access points and biologist recommendations. We confined sampling at each site to a designated river segment (≤5.0 river kilometres); however, silver carp were collected from three river segments in the Illinois River and two in the Wabash River that were distributed between 6.1 and 43.1 rkm apart due to both limited access points and low localised catch rates. Because silver carp home ranges are generally <70 rkm (Prechtel et al., 2018), data from these segments were pooled and considered a single site within each river for analysis.

At each site, we collected silver carp using daytime boat electroshocking (Smith-Root [Des Moines and Missouri river sites only] or MBS-1D Wisconsin style control box; DC; 4~13 amps, 100~500 V, 60 pulses per second with two netters) surveys focusing on side-channel, channel border, and backwater habitats. Electrofishing surveys employed a “standardize by power” approach (e.g., Miranda, 2009) to ensure that a constant amount of power was being transferred to the fish across variable water conductivities. Per sampling trip, we collected silver carp from two to three spatially independent

**TABLE 1** Characteristics of the nine study sites used to assess spatial variation in silver carp population ecology throughout the upper Mississippi River. We obtained air temperature data from National Oceanic and Atmospheric Administration (NOAA) gauging stations and daily discharge data from U.S. Geological Survey gauging stations. We obtained the year and time since the first silver carp was detected at or adjacent to (<70 rkm) each study site from the Nonindigenous Aquatic Species Database (2020). Map identification numbers correspond to numbered locations in Figure 1.

<table>
<thead>
<tr>
<th>Map no.</th>
<th>Site</th>
<th>Site characteristics</th>
<th>Mean daily air temperature (°C)</th>
<th>Mean daily river discharge (m³/s)</th>
<th>First silver carp detection</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Missouri R.</td>
<td>41°36′19″ N 96°06′48″ W</td>
<td>10.6</td>
<td>1,045.1</td>
<td>2003 12</td>
</tr>
<tr>
<td>2</td>
<td>Des Moines R.</td>
<td>40°23′11″ N 91°26′11″ W</td>
<td>8.3</td>
<td>323.4</td>
<td>1986 29</td>
</tr>
<tr>
<td>3</td>
<td>Upper Illinois R.</td>
<td>41°19′38″ N 88°52′09″ W</td>
<td>8.5</td>
<td>461.1</td>
<td>1999 16</td>
</tr>
<tr>
<td>4</td>
<td>Middle Illinois R.</td>
<td>40°09′47″ N 90°11′57″ W</td>
<td>8.1</td>
<td>550.1</td>
<td>1998 17</td>
</tr>
<tr>
<td>5</td>
<td>Illinois R. Confluence</td>
<td>38°55′59″ N 90°28′28″ W</td>
<td>11.1</td>
<td>6,556.6</td>
<td>1998 17</td>
</tr>
<tr>
<td>6</td>
<td>Middle Mississippi R.</td>
<td>37°15′08″ N 89°30′14″ W</td>
<td>14.0</td>
<td>7,247.9</td>
<td>1983 32</td>
</tr>
<tr>
<td>7</td>
<td>Lower Mississippi R.</td>
<td>36°34′41″ N 89°31′19″ W</td>
<td>11.8</td>
<td>7,247.9</td>
<td>1982 33</td>
</tr>
<tr>
<td>8</td>
<td>Lower Wabash R.</td>
<td>38°07′51″ N 87°56′36″ W</td>
<td>11.4</td>
<td>1,014.2</td>
<td>1986 29</td>
</tr>
<tr>
<td>9</td>
<td>Upper Wabash R.</td>
<td>39°06′36″ N 87°39′15″ W</td>
<td>13.2</td>
<td>427.9</td>
<td>1999 16</td>
</tr>
</tbody>
</table>
electrofishing surveys within each site, where survey boundaries did not overlap. We conducted between two and five boat electrofishing surveys at all but two sites: we conducted only one survey at the Middle Mississippi River site while we conducted a total of 15 surveys at the Des Moines River Confluence site. We measured silver carp length (total length [TL]; 1 mm), weight (1.0 kg), and removed lapillar otoliths for age and growth analysis (Seibert & Phelps, 2013). We wiped removed otoliths clean and stored them individually in scintillation vials.

Otoliths were air-dried at room temperature for at least four weeks following collection. Dried otoliths were embedded in epoxy resin and sectioned (approximately 0.8-mm thick) along the transverse plane through the nucleus using a low-speed saw (Buehler® Isomet® 1,000 Precision Saw) with a 0.4 mm diamond wafer blade. When dry, we polished each side of the cross-section using wetted 2,000-grit sandpaper and placed the section in a petri dish with immersion oil to improve clarity. We examined all otolith cross-sections using a dissecting microscope with transmitted light under 20-50x magnification. Two experienced readers independently aged otoliths with no knowledge of fish length, estimated age of the otolith by the other reader, or source-river. Both readers assessed the otolith jointly if a consensus age could not be obtained. Using only otoliths with consensus ages, we captured a digital image of each otolith using an Olympus SZX7 microscope (model no. PL-A6662) and ImagePro Plus image analysis software (version 7.0; Media Cybernetics). We then measured the distance from the primordium to each annual ring along the sulcal transect for each otolith.

2.3 Calculation of population characteristics and determining spatial differences

We indexed silver carp relative abundance as the average boat electrofishing catch per unit effort (CPUE; mean fish/hr) at each site where we conducted two or more electrofishing surveys. We sampled silver carp from April through November across all sites; a majority (79.7%) of carp were collected after June and throughout multiple months at all sites except the Missouri River and Illinois River Confluence sites where we sampled carp during a single sampling trip in August. Silver carp catch rates vary temporally and are high during May-June (Sullivan et al., 2017), but collections across multiple months and only during August, when catch rates are lowest, likely led to conservative

FIGURE 1 Locations of the nine study sites used to assess spatial variation in silver carp population ecology throughout the upper Mississippi River. The number next to each study site corresponds to map identification numbers in Table 1.
estimates of catch per unit effort across sites. We examined spatial differences in silver carp CPUE using an analysis of variance (ANOVA) with site as a fixed effect. If significant differences were detected, we used Tukey’s honest significant difference (HSD) test to determine specific among-site differences.

We evaluated silver carp condition at each site using a length-weight relationship (Ricker, 1975). We used analysis of covariance (ANCOVA) to determine whether differences in weight at a given length varied among sampling sites using length as a covariate; both weight and length were log-transformed (log<sub>10</sub>) prior to the analysis. We inspected residuals graphically using a quantile-quantile (QQ) plot and model fit was deemed adequate. We predicted the log<sub>10</sub>-weight and 95% confidence interval for an arbitrary 600 mm TL (2.778 mm log<sub>10</sub>TL; BW600) silver carp (mid-sized adult; Figure S1) at each site to compare patterns in condition without the confounding effect of length (Cone, 1989). We extracted silver carp BW600 predictions from the ANCOVA results using the "lsmeans" function and used Tukey’s HSD test ("cld" function) to determine if BW600 predictions significantly differed among sites at a significance level α of 0.05 using the "multcomp" tools package (Hothorn et al., 2008). Silver carp log<sub>10</sub>weight predictions (BW600) were back-transformed into standard units for interpretation.

We calculated silver carp size structure for each site using proportional size distribution (PSD) for preferred (PSD-P; ≥560.0 mm) and memorable (PSD-M; ≥740.0 mm) size-classes following Phelps and Willis (2013). Silver carp ≤ 560.0 mm and ≥ 929.9 mm composed a small proportion of overall catch across sites (18% and 0.01%, respectively) and were not present at all sites, precluding the calculation of other PSD indices. We estimated confidence intervals (95%) for PSD-P and PSD-M using a binomial distribution (Gustafson, 1988; Ogle, 2016), where the number of samples equalled the total catch at each site. We then used a chi-square test of independence to determine if differences occurred in PSD-P and PSD-M among sites; if a difference was detected, pairwise chi-square tests were conducted to determine site-specific differences.

Using site-specific age-frequency distributions, we evaluated inter-annual recruitment variability using the recruitment variability index (RVI; Guy & Willis, 1995) calculated as

\[
RVI = \left[ S_n \div (N_M + N_p) \right] - \left( N_M \div N_p \right)
\]

where \( S_n \) is the sum of the cumulative relative frequencies across year-classes in the sample, \( N_M \) is the number of missing year-classes from the sample (year-classes beyond the oldest year-class in the sample are excluded), \( N_p \) is the total number of year-classes present in the sample. Values of RVI range from -1.0 to 1.0, with values closer to 1.0 indicating more stable recruitment. Using weighted regression, we estimated total annual mortality rates (A) of silver carp populations collected at each site (i.e., catch-curve; Maceina & Bettoli, 1998). Instantaneous mortality rates (Z) are commonly estimated using the slope of the descending limb of the age-frequency histogram (i.e., a catch-curve analysis): the antilog of Z corresponds to the annual survival rate (S), and 1-S is equal to A. We used the peak abundance at each site as the first age-group used for the catch-curve analysis (Smith et al., 2012), corresponding to age 6 or 7 silver carp. Differences in mortality rates could be attributed to both natural and fishing-induced mortality, as variable amounts of commercial harvest occur across sites (e.g., Jones & Gritters, 2012; Maher, 2017) and rates herein likely reflect both sources of mortality. To determine if A differed among sites, we used an ANCOVA to test for differences in catch-curve slopes using site and age as covariates; if differences among sites were detected, Tukey’s HSD test was used to determine which sites differed at a significance level α of 0.05.

We estimated silver carp growth trajectories at each site using von Bertalanffy models fit to individual length at estimated age data with nonlinear least-squares regression:

\[
L_t = L_\infty \left( 1 - e^{-K(t-t_0)} \right)
\]

where \( L_t \) = mean length-at-age at time \( t \), \( L_\infty \) = mean maximum length, \( K \) = instantaneous rate at which \( L_\infty \) approaches \( L_\infty \), and \( t_0 \) is the x-intercept. Models were fit using the Fisheries Stock Analysis (FSA) package (version 0.8.19; Ogle, 2016) and we obtained all starting parameter values by visually fitting the von Bertalanffy growth function to the observed data. All parameters predicted from each model were summarised with bootstrap confidence intervals using the "nlsBoot" function from the "nlsTools" package (described by Ogle, 2016). We compared estimates of silver carp growth parameters among sites using Akaike’s information criterion corrected for small sample size (AIC<sub>c</sub>) and associated delta AIC<sub>Δ</sub> values. Only models with \( \Delta \) values <2.0 or \( w_i \) value >0.1 were used for interpretation (Burnham & Anderson, 2003).

We used Pearson’s product moment correlations (Pearson’s r) to explore relationships among silver carp population characteristics across sites: CPUE (fish/hr), BW600, RVI, A, PS-P, PS-M, maximum age, \( L_\infty \), and K. We did not estimate the correlation between \( L_\infty \) and K since these parameters are mathematically related (e.g., Motulsky & Christopoulos, 2003). We also examined correlations between latitude and time since first detection (years) with all silver carp population characteristics. Using the Nonindigenous Aquatic Species Database (2020), we estimated the number of years since the first silver carp was detected at or adjacent to (<70 rkm; Prechtel et al., 2018) each site (time since first detection [years]). p-values were generated using the "rcorr" function from the "Hmisc" tools package to determine if relationships existed between population characteristics. All analyses were performed in Program R Software Version 3.2.0 (R Core Team, 2019) using an α of 0.05; Bonferroni-corrected p-values were used to determine if relationships were statistically significant.

### 2.4 Evaluating the role of abiotic variables on mean length at age of silver carp

Using the measured distances between annuli, we constructed age-growth curves for individual silver carp by calculating annual
length-at-age estimates using the Fraser-Lee direct proportional method:

\[ L_i = a + (L_c - a) \left( \frac{S_i}{S_c} \right) \]  

(3)

where \( L_i \) is the length at time \( i \), \( L_c \) is the length at capture, \( S_i \) is the otolith radius at time \( i \), \( S_c \) is the otolith radius at the time of capture, and \( a \) is the site-specific intercept of the regression between fish length and otolith radius (i.e., biological intercept). We used silver carp length at age 3 to compare growth rates among populations since carp mature at age-3 or older (Kolar et al., 2007) and most of the aged carp were age-4 or older. We averaged length at age 3 for each site and each year-class present at each site; for example, mean silver carp length at age 3 was estimated separately for age-5 and age-6 carp from a site. In all, we averaged silver carp length at age 3 for five to eight year-classes at each site, depending on the range of year-classes present in the sample (total = 57 total mean length at age 3 estimates across all sites).

Using linear mixed-effects models, we evaluated the effects of river discharge and temperature predictors on silver carp mean length at age 3 across all sites and year-classes. River discharge and temperature data spanned from 2006 to 2014 as these years represented the period where silver carp were estimated to be between ages 1 and 3 across sites. We obtained river discharge data from U.S. Geological Survey (USGS; https://usgs.gov/; last accessed on March 20, 2020) gauging stations located closest to our study sites, either upstream or downstream, and restricted data to April 1st to October 31st as winter discharge data were infrequently reported. We calculated river base discharge (BASE.FLOW; 7-day minimum/mean discharge for a year), the ordinal date of maximum river discharge, and SS metrics because they represent the general lower and upper bounds of preferred temperatures for silver carp and closely related bighead carp *H. nobilis* (see Kolar et al., 2007). We also calculated the mean temperature during the first three years of life (TEM; from January 1st to December 31st). Except for TEM, variables represented conditions during the first year of life since growth early in life can have lasting effects on adult population demographics (Jonsson & Jonsson, 2014). We created the predictor variables so each was biologically relevant and represented a different river condition that may affect silver carp growth rates.

We built models using site as a random effect and additive combinations of the four discharge and four temperature variables as fixed effects, using the "lme4" tools package in Program R. We included a random intercept for each site, allowing silver carp populations at each site to have higher or lower than average growth. We checked for multicollinearity among predictor variables by calculating the variance inflation factor (VIF) for each variable using the "vif" function from the "car" tools package; there was no evidence for multicollinearity as all VIFs were ≤2.5, which is lower than conventional cut-offs (e.g., Midi & Bagheri, 2010), and all variables were included.

We assessed normality and homoscedasticity of predictor variables a priori using normal quantile and residual plots from the fitted model; we log10 transformed values for the SS and HIGH metrics to normalise residuals. We used maximum likelihood (ML) parameter estimates instead of restricted maximum likelihood (REML; default) estimates since REML estimates are not comparable when fixed effects differ among models (Zuur et al., 2009). We calculated Akaike’s information criterion corrected for small sample size (AICc) and associated delta AICc (\( \Delta_\text{AICc} \)) and Akaike weights (\( w_i \)) to rank models based on their relative support for the data. We only used models with \( \Delta_\text{AICc} \) values <2.0 or \( w_i \) values >0.1 for interpretation (Burnham & Anderson, 2003).

3 | RESULTS

3.1 | Spatial differences in population characteristics and their correlations

Electrofishing surveys captured 52–259 silver carp at each site (1,104 total captures; Table 2). Silver carp CPUE was highest at the Middle Mississippi River site (155 fish/hr), but only one electrofishing survey was conducted and was excluded from the CPUE analysis. Across sites with two or more electrofishing surveys, mean silver carp CPUE ranged from 10 to 77 fish/hr (Figure 2). Catch per unit effort was highly variable within sites and was not different among sites (\( F_{10,23} = 0.47, p = .89 \)). Silver carp mean total length (TL; mm) ranged from 532 to 707 mm (Table 2; Figure S1) and PSD-P and PSD-M differed among sites (PSD-P: chi-square = 664.1, \( p < .001 \); PSD-M: chi-square = 72.2, \( p < .001 \)). Silver carp PSD-P was greater at the Des Moines River Confluence, Lower Mississippi River, and both Wabash River sites compared to other sites, whereas silver carp PSD-P was lowest at the Missouri River site (Figure 2). Silver carp PSD-M was highest at the Wabash River sites and lower at the Middle Illinois River and Illinois River Confluence sites (Figure 2). Mean predicted weight of a 600 mm TL silver carp was lowest at the Lower and Middle
TABLE 2  Summary statistics describing the total number (N), minimum, maximum, and mean (±1 SE) total length (TL; mm) and estimated age (years) of captured silver carp from the nine upper Mississippi River study sites. We report the number of boat electrofishing transects conducted per site (N). Map identification numbers correspond to numbered locations in Figure 1.

<table>
<thead>
<tr>
<th>Map no.</th>
<th>Site</th>
<th>Electrofishing transects (N)</th>
<th>Total length (TL; mm)</th>
<th>Age (years)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>N</td>
<td>Mean (±1 SE)</td>
</tr>
<tr>
<td>1</td>
<td>Missouri R.</td>
<td>2</td>
<td>151</td>
<td>532 (±4)</td>
</tr>
<tr>
<td>2</td>
<td>Des Moines R. Confluence</td>
<td>15</td>
<td>259</td>
<td>676 (±3)</td>
</tr>
<tr>
<td>3</td>
<td>Upper Illinois R.</td>
<td>3</td>
<td>54</td>
<td>576 (±7)</td>
</tr>
<tr>
<td>4</td>
<td>Middle Illinois R.</td>
<td>5</td>
<td>52</td>
<td>571 (±8)</td>
</tr>
<tr>
<td>5</td>
<td>Illinois R. Confluence</td>
<td>2</td>
<td>126</td>
<td>582 (±6)</td>
</tr>
<tr>
<td>6</td>
<td>Middle Mississippi R.</td>
<td>1</td>
<td>103</td>
<td>593 (±16)</td>
</tr>
<tr>
<td>7</td>
<td>Lower Mississippi R.</td>
<td>2</td>
<td>93</td>
<td>683 (±6)</td>
</tr>
<tr>
<td>8</td>
<td>Lower Wabash R.</td>
<td>2</td>
<td>120</td>
<td>707 (±5)</td>
</tr>
<tr>
<td>9</td>
<td>Upper Wabash R.</td>
<td>3</td>
<td>146</td>
<td>678 (±7)</td>
</tr>
</tbody>
</table>

Mississippi River sites and highest at the Wabash River sites, where predicted weight ranged from 2.02 kg (95%: 1.99–2.07: Lower Mississippi River site) to 2.52 kg (95%: 2.48–2.56: Lower Wabash River; Figure 2). Silver carp length-weight relationships varied among sites (ANCOVA test for differences among sites: F8,1049 = 3.05, p = .002) and the significant fish length and site interaction (F8,1,049 = 3.29, p = .001) indicates that the effect of silver carp length on weight differs across sites (Figure S2). A post hoc Tukey test found that silver carp at the Missouri River site (all weighed more at a given length than silver carp captured at the Middle Illinois River site (all p < .05). Further, silver carp at the Upper Wabash River site weighed more at a given length than silver carp captured at the Missouri River site (p = .04).

A total of 847 silver carp were aged, ranging from 48 to 133 individuals per site (Table 2). Total annual mortality rates (A) did not differ across sites (ANCOVA test for differences in catch-curve slopes among sites: F8,16 = 1.16, p = .34); A ranged from 0.40 (95%; 0.16–0.65: Lower Wabash River) to 0.67 (95%; 0.22–0.88: Des Moines River Confluence; Figure 2). Recruitment variability index (RVI) ranged from 0.66 to 0.95, indicating that recruitment tended to be relatively stable across sites. We observed distinct spatial differences in silver carp length-at-age predicted from von Bertalanffy growth models. Estimates of silver carp L∞, K, and t₀ varied across sites (AICc = 60,846.4, Δ₁ = 0, w₀ = 0.99), indicating that growth potential is variable across the UMR (Figure 3; Table 3). There was a difference of nearly 200 mm in the estimated maximum mean length (L∞) across sites, ranging from 601 mm TL (Missouri River) to 772 mm TL (Des Moines River Confluence). The Brody growth coefficient (K) ranged from 0.22 (Illinois River Confluence) to 0.30 (Lower Wabash River; Table 3).

Silver carp RVI was negatively correlated with CPUE (fish/hr; Pearson’s r = −.77, p = .01) and time since first detection (Pearson’s r = −.76, p = .02; Figure 4). Silver carp maximum estimated age was negatively correlated with latitude (Pearson’s r = −.69, p = .04; Figure 4); all other correlations were not significant (all p > .05).

### 3.2 Influence of abiotic variables on mean length at age 3

After evaluating all additive model combinations, the most parsimonious model (AICc = −153.7, w₀ = 0.17; Table 4) indicated that mean silver carp length at age 3 was positively associated with the coefficient of variation (CV) of mean daily discharge (m³/s; model coefficient = 0.001, 95%: 0.001 to 0.002), ordinal date of maximum discharge (ORD; model coefficient = 0.0005, 95%: 0.0002 to 0.0009), and mean May-June temperature (TMAY; model coefficient = 0.019, 95%: 0.012 to 0.026; Figures S3–S5). Individual fixed effects, however, indicated that a 50% increase in the coefficient of variation (CV) of mean daily discharge (m³/s) only resulted in a 0.05 mm TL increase in silver carp length at age 3, a 1°C increase in mean May-June temperatures only resulted in a 0.02 mm TL increase, and maximum discharge 60 days later in the year only resulted in a 0.03 mm TL increase in silver carp length at age 3. Thus, the covariate effects on silver carp length at age 3 were not biologically relevant.

The second most supported model (Δ₁ = 1.14, w₀ = 0.10) indicated that mean silver carp length at age 3 was positively associated with the coefficient of variation (CV) of mean daily discharge (m³/s; model coefficient = 0.002, 95%: 0.001 to 0.002), ordinal date of maximum discharge (ORD; model coefficient = 0.0005, 95%: 0.0002 to 0.0009), and mean May-June temperature (TMAY; model coefficient = 0.019, 95%: 0.012 to 0.026). This model also included base flow discharge (BASE.FLOW; model coefficient = 0.070, 95%: −0.041 to 0.181), but the regression coefficient confidence interval overlapped zero and was not interpreted. The third (Δ₁ = 1.46, w₀ = 0.08) and fourth (Δ₁ = 1.68, w₀ = 0.07) most supported models...
both indicated that mean silver carp length at age 3 was positively associated with the coefficient of variation (CV) of mean daily discharge (m³/s), ordinal date of maximum discharge (ORD), and mean May-June temperature (TMAY). The third most supported model also included the median number of high pulse days (HIGH; model coefficient = 0.00003, 95%: −0.0003 to 0.0003) and the fourth model also included the number of days below freezing (DBF; model coefficient = −0.0005, 95%: −0.0015 to 0.0005), but both

**FIGURE 2** Silver carp population characteristics for nine study sites throughout the upper Mississippi River. Shown are the (a) mean catch per unit effort (CPUE; fish/hr), (b) mean predicted weight (kg) of a 600 mm total length (TL) silver carp (BW600), (c) proportional size distribution of preferred length silver carp (PSD-P; 560.0–739.9 mm), (d) proportional size distributions of memorable length silver carp (PSD-M; 740.0–929.9 mm), and (e) total annual silver carp mortality rates (A) for each site. Error bars represent 95% confidence intervals, and statistical significance is indicated by differences in letters above bars. Asterisks denote study sites where only one electrofishing survey occurred. The number next to each study site corresponds to map identification numbers in Table 1

**FIGURE 3** Silver carp von Bertalanffy growth curves for nine study sites throughout the upper Mississippi River. Shown are the fits to the length-at-age data for each population using the von Bertalanffy growth equation. The number next to each study site corresponds to map identification numbers in Table 1

<table>
<thead>
<tr>
<th>Map no.</th>
<th>Site</th>
<th>L∞</th>
<th>K</th>
<th>t₀</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Missouri R.</td>
<td>601 (578–629)</td>
<td>0.30 (0.26–0.34)</td>
<td>−0.49 (−0.67 to −0.33)</td>
</tr>
<tr>
<td>2</td>
<td>Des Moines R. Confluence</td>
<td>772 (752–795)</td>
<td>0.24 (0.22–0.26)</td>
<td>−0.38 (−0.50 to −0.27)</td>
</tr>
<tr>
<td>3</td>
<td>Upper Illinois R.</td>
<td>691 (656–744)</td>
<td>0.28 (0.22–0.33)</td>
<td>−0.73 (−1.06 to −0.44)</td>
</tr>
<tr>
<td>4</td>
<td>Middle Illinois R.</td>
<td>740 (696–801)</td>
<td>0.23 (0.19–0.28)</td>
<td>−0.69 (−1.02 to −0.42)</td>
</tr>
<tr>
<td>5</td>
<td>Illinois R. Confluence</td>
<td>764 (732–806)</td>
<td>0.22 (0.19–0.25)</td>
<td>−0.67 (−0.87 to 0.48)</td>
</tr>
<tr>
<td>6</td>
<td>Middle Mississippi R.</td>
<td>746 (713–788)</td>
<td>0.25 (0.22–0.29)</td>
<td>−0.64 (−0.87 to −0.44)</td>
</tr>
<tr>
<td>7</td>
<td>Lower Mississippi R.</td>
<td>687 (656–727)</td>
<td>0.28 (0.24–0.32)</td>
<td>−0.50 (−0.73 to 0.30)</td>
</tr>
<tr>
<td>8</td>
<td>Lower Wabash R.</td>
<td>706 (680–738)</td>
<td>0.30 (0.25–0.34)</td>
<td>−0.80 (−1.06 to −0.57)</td>
</tr>
<tr>
<td>9</td>
<td>Upper Wabash R.</td>
<td>711 (681–750)</td>
<td>0.27 (0.23–0.32)</td>
<td>−0.84 (−1.12 to −0.61)</td>
</tr>
</tbody>
</table>

TABLE 3 Mean asymptotic length (L∞), Brody-Bertalanffy growth coefficient (K), the age when mean silver carp length is zero (t₀), and lower and upper bounds of 95% confidence intervals calculated from the estimated otolith ages obtained from silver carp captured from the nine upper Mississippi River study sites. Map identification numbers correspond to numbered locations in Figure 1.
FIGURE 4 Relationships between silver carp recruitment variability index (RVI) and both catch per unit effort (CPUE [fish/hr]; a) and the time since first detection (years; b), and between latitude and the maximum estimated silver carp age (c) for nine study sites throughout the upper Mississippi River.
Silver carp populations in the UMR and several authors attribute lower silver carp abundance, and therefore fish that are larger and in better condition, to less niche space available for populations to reach high abundances (e.g., Pyron et al., 2017; Stuck et al., 2015). In the dammed Missouri, Des Moines, Illinois, and Mississippi rivers where native species populations have declined (e.g., Wiener et al., 1998), silver carp population abundance was high and population characteristics were drastically different than those estimated for the Wabash River populations. In addition to intraspecific competition, silver carp compete with native planktivores, such as gizzard shad Dorosoma cepedianum and bigmouth buffalo Ictiobus cyprinellus (e.g., Irons et al., 2007; Pendleton et al., 2017). In river reaches where silver carp are highly abundant and compose a greater proportion of the fish community than other planktivores (high intra- and interspecific competition), carp condition and density are inversely related (Coulter, MacNamara, et al., 2018), suggesting or recently colonised species can exhibit differential population ecology when establishing vs. when invading (e.g., Fox et al., 2007; Rypel, 2014), it is important to consider the invasion history when assessing invasive species ecology.

Silver carp populations are spatially structured in the UMR and intra- or interspecific competition could lead to the variation in silver carp abundance, condition, and growth rates exhibited herein. Similar to Stuck et al. (2015), silver carp populations in the Wabash River, a largely free-flowing river with minimal anthropogenic modifications, were less abundant, larger, weighed more, older, faster-growing, and exhibited lower mortality rates compared to populations in other dam-influenced rivers. Native fish assemblages are more intact in the free-flowing Wabash River than in impounded reaches of the UMR and several authors attribute lower silver carp abundance, and therefore fish that are larger and in better condition, to less niche space available for populations to reach high abundances (e.g., Pyron et al., 2017; Stuck et al., 2015). In the dammed Missouri, Des Moines, Illinois, and Mississippi rivers where native species populations have declined (e.g., Wiener et al., 1998), silver carp population abundance was high and population characteristics were drastically different than those estimated for the Wabash River populations. In addition to intraspecific competition, silver carp compete with native planktivores, such as gizzard shad Dorosoma cepedianum and bigmouth buffalo Ictiobus cyprinellus (e.g., Irons et al., 2007; Pendleton et al., 2017). In river reaches where silver carp are highly abundant and compose a greater proportion of the fish community than other planktivores (high intra- and interspecific competition), carp condition and density are inversely related (Coulter, MacNamara, et al., 2018), suggesting

4 | DISCUSSION

Our study represents the first to compare silver carp population ecology across areas where they have been present for over a decade (see Stuck et al., 2015) and identify how invasion history and population-habitat linkages affect populations. Despite invasive silver carps’ known inhabitance of the UMR since the early 1980s (Nonindigenous Aquatic Species, 2020), evaluations of carp population ecology began in the early 2000s, likely because their catch was previously low and sparse (e.g., DeBoer et al., 2018; Irons et al., 2007). Early evaluations in the Middle Mississippi River and mainstem Missouri River suggested that silver carp were fast growing and reached large sizes (Wanner & Klumb, 2009; Williamson & Garvey, 2005); more contemporary evaluations in the Missouri River tributaries in eastern South Dakota (Hayer et al., 2014) and impoundments in the lower Tennessee and Cumberland rivers (Ridgway & Bettoli, 2017) have reported similar findings. Interestingly, all study sites were in river reaches at times when silver carp were first detected ≤10 years before the initiation of their study and reported that carp populations were composed of fish that were younger, faster-growing, and larger at a given age than populations reported herein. Because invasive or recently colonised species can exhibit differential population ecology when establishing vs. when invading (e.g., Fox et al., 2007; Rypel, 2014), it is important to consider the invasion history when assessing invasive species ecology.

Silver carp populations are spatially structured in the UMR and intra- or interspecific competition could lead to the variation in silver carp abundance, condition, and growth rates exhibited herein. Similar to Stuck et al. (2015), silver carp populations in the Wabash River, a largely free-flowing river with minimal anthropogenic modifications, were less abundant, larger, weighed more, older, faster-growing, and exhibited lower mortality rates compared to populations in other dam-influenced rivers. Native fish assemblages are more intact in the free-flowing Wabash River than in impounded reaches of the UMR and several authors attribute lower silver carp abundance, and therefore fish that are larger and in better condition, to less niche space available for populations to reach high abundances (e.g., Pyron et al., 2017; Stuck et al., 2015). In the dammed Missouri, Des Moines, Illinois, and Mississippi rivers where native species populations have declined (e.g., Wiener et al., 1998), silver carp population abundance was high and population characteristics were drastically different than those estimated for the Wabash River populations. In addition to intraspecific competition, silver carp compete with native planktivores, such as gizzard shad Dorosoma cepedianum and bigmouth buffalo Ictiobus cyprinellus (e.g., Irons et al., 2007; Pendleton et al., 2017). In river reaches where silver carp are highly abundant and compose a greater proportion of the fish community than other planktivores (high intra- and interspecific competition), carp condition and density are inversely related (Coulter, MacNamara, et al., 2018), suggesting

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**TABLE 4** Linear mixed-effects model selection results for models evaluating predictors of mean silver carp length at age 3 across the nine study sites in the upper Mississippi River. The table includes the model fixed effects, number of parameters, maximum likelihood estimates, Akaike’s information criterion corrected for small sample size (AICc), the difference between the AICc value of the most parsimonious model and model i (Δi), and the relative support for model i (Akaike weight [wi]). We evaluated all possible additive model combinations, but only interpreted models with Δi > 2.0 or wi < 0.1. The top 5 of 256 models assessed are presented below, along with the intercept only model.

<table>
<thead>
<tr>
<th>Model fixed effects</th>
<th>No. of parameters</th>
<th>Maximum likelihood</th>
<th>AICc</th>
<th>Δi</th>
<th>wi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Daily Discharge Coefficient of Variation (CV) + Maximum Discharge Ordinal Date (ORD) + Mean May-June Temperature (TMAY)</td>
<td>6</td>
<td>83.7</td>
<td>-153.7</td>
<td>0.00</td>
<td>0.17</td>
</tr>
<tr>
<td>Base Flow (BASE.FLOW) + Daily Discharge Coefficient of Variation (CV) + Maximum Discharge Ordinal Date (ORD) + Mean May-June Temperature (TMAY)</td>
<td>7</td>
<td>84.4</td>
<td>-152.6</td>
<td>1.14</td>
<td>0.10</td>
</tr>
<tr>
<td>Median Number of High Pulse Days (HIGH) + Daily Discharge Coefficient of Variation (CV) + Maximum Discharge Ordinal Date (ORD) + Mean May-June Temperature (TMAY)</td>
<td>7</td>
<td>84.3</td>
<td>-152.3</td>
<td>1.46</td>
<td>0.08</td>
</tr>
<tr>
<td>Days Below Freezing (DBF) + Daily Discharge Coefficient of Variation (CV) + Maximum Discharge Ordinal Date (ORD) + Mean May-June Temperature (TMAY)</td>
<td>7</td>
<td>84.1</td>
<td>-152.1</td>
<td>1.68</td>
<td>0.07</td>
</tr>
<tr>
<td>Summer Severity (SS) + Daily Discharge Coefficient of Variation (CV) + Maximum Discharge Ordinal Date (ORD) + Mean May-June Temperature (TMAY)</td>
<td>7</td>
<td>83.7</td>
<td>-151.3</td>
<td>2.45</td>
<td>0.05</td>
</tr>
<tr>
<td>Intercept</td>
<td>3</td>
<td>71.7</td>
<td>-136.9</td>
<td>16.86</td>
<td>0.00</td>
</tr>
</tbody>
</table>
density-dependent controls on populations. We did not detect a relationship between silver carp abundance and body weight, growth, or mortality because carp catch rates were highly variable and we may have lacked statistical power. That both intra- and interspecific competition structure silver carp populations and contribute to population spatial heterogeneity is, however, likely.

Growth rates and maximum fish size and age can increase with increasing latitude (e.g., Weber et al., 2015), where either genetic adaptations (i.e., fish at higher latitudes grow faster; Levinton, 1983) or higher growth rates during the growing season (i.e., counter-gradient variation in growth; Bergmann, 1847) are hypothesised to drive these relationships. Neither silver carp growth rates nor maximum fish size were associated with latitude herein. Silver carp populations from the higher-latitude Missouri River and Upper Illinois River sites did exhibit some of the highest growth rates, but populations from a similar latitude displayed low growth rates. The influence of latitude on silver carp population ecology cannot be ruled out, but we suggest that other factors are more likely to contribute to the observed trends. As previously discussed, intra- and interspecific competition and river characteristics likely lead to spatial variation in silver carp populations; however, the negative relationship between silver carp maximum age and latitude could also be explained by movement patterns. Coulter et al. (2020) reported that smaller silver carp moved more frequently over greater distances in areas where carp are established, suggesting that smaller mature carp, and thereby younger fish, frequently move upstream, but size-specific movement patterns may also be river-specific (see Prechtel et al., 2018). Further, latitude and the time since first detection are moderately correlated since the silver carp invasion progressed gradually upstream, and some relationships can therefore be confounded. Our study focused on areas that were separated by distances that exceed the known silver carp home-range size, but some interdependency among populations in the UMR could prohibit identifying large-scale trends, emphasising the need for evaluating populations physically separated in other latitudes or experiment-based evaluations to validate the existence of a latitudinal response.

More stable silver carp recruitment (indexed using RVI) was associated with lower catch per unit effort and less time since the first carp was detected at a site, providing evidence for the incorporation of invasion history into population assessments and further explaining spatiotemporal patterns in recruitment (Chick et al., 2020; Larson et al., 2017; Sullivan et al., 2018). Fish recruitment can decrease with increasing density (Rose et al., 2001), suggesting that compensatory density-dependent processes may govern silver carp recruitment. Despite fluctuations in adult silver carp populations (e.g., Chick et al., 2020) and commercial harvest (e.g., MacNamara et al., 2016), carp have persisted throughout the UMR. If compensatory responses were not present, any increase in mortality (i.e., harvest) would eventually result in population decline because mortality would exceed recruitment. Further, for expanding species, we expect individuals with better dispersal or colonising traits (larger, more reproductive output) to dominate more recently invaded areas (e.g., Azzurro et al., 2016; Fox et al., 2007; Sakai et al., 2001), suggesting that populations in recently invaded habitats are different than those in longer-established habitats via compensatory density-dependent processes. For instance, silver carp recruitment was most stable in the Illinois River where commercial harvest is highest (Asian Carp Regional Coordinating Committee, 2017; MacNamara et al., 2016) and carp were first detected <20 years ago. We know of no other published data documenting silver carp recruitment variability in response to their abundance and invasion history. Although many questions remain to be answered about the association between silver carp recruitment and their invasion history, it is evident that the invasion context can play a key role in driving variability in carp populations.

We hypothesised that high discharges and May-June temperatures would be positively related to silver carp mean length at age 3 but found little support for this hypothesis. Model selection indicated silver carp mean length at age 3 was positively associated with warmer water temperatures during May-June, more variable discharges, and peaks in discharge later during the summer. The coefficients and effect sizes of these parameters were, however, small; and large increases in water temperature, discharge variability, and timing were estimated to have minor effects on silver carp length at age 3 (<1 mm) that were not biologically meaningful. Scatterplots suggested there may be different slopes between silver carp mean length at age 3 and these three covariates among sites, but limited sample sizes prohibited us from testing these effects. Understanding how these relationships may potentially vary among locations would provide an advancement in understanding invasive carp populations and remains an area for further investigation.

Silver carp commercial harvest effort varies across the UMR and can be extensive in some areas, potentially influencing populations. Selective fish harvest, like commercial fishing, can change fish population characteristics via size-selective mortality with resulting changes to growth (Quist et al., 2002), mortality (Heino & Godø, 2002), size structure (Olden et al., 2007), fecundity (Arlinghaus et al., 2009), and maturation schedules (Dunlop et al., 2018). Silver carp populations are commercially harvested within the river reaches upstream from our Illinois River sampling sites (Asian Carp Regional Coordinating Committee, 2017; Irons et al., 2007); where invasion into the Great Lakes watershed is most likely to occur. Despite varying harvest of silver carp throughout the UMR, we do not believe commercial fishing largely influenced our results. MacNamara et al. (2016) found that silver carp population characteristics can remain stable despite high harvest levels in the Illinois River, suggesting that high immigration from neighbouring areas or compensatory survival can maintain population characteristics. Further, Tsehaye et al. (2013) concluded that silver carp populations can be controlled with commercial harvest, but requires consistent, targeted, and high levels of harvest, which does not occur at our study areas (occurs upstream of Illinois River sampling sites). In areas where immigration may be limited and large numbers of silver carp are removed annually (e.g., >500,000 adult bigheaded carp were removed from stretches of the Upper Illinois River during 2010–2017; Asian Carp Regional Coordinating Committee, 2017), potential changes in population characteristics associated with harvest deserve further attention.
Our study illustrated that, once established, invasive silver carp recruitment is less stable in more abundant and longer-established populations. We suggest that, because silver carp populations inhabiting nearby rivers at similar latitudes can exhibit drastically different population characteristics, intra- and interspecific interactions and carp movement patterns may contribute to the spatial heterogeneity of populations. River conditions throughout the UMR are inherently less variable than the historic free-flowing river conditions but may change in both timing and predictability as climate change progresses (Arnell & Gosling, 2014). Future changes in river conditions could favour silver carp and result in changes to biotic interactions with native species. To conserve and promote native biodiversity within the UMR, mitigating the effects of silver carp via increased harvest or restricting their movement (e.g., physical or nonphysical barriers) is of the utmost importance. Our study helps further disentangle silver carp population ecology in the UMR, but developing effective mitigative strategies will require better information regarding the interspecific interactions between carp and native species and how these interactions may change in response to environmental conditions, invasion context, and mitigation efforts.

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CONFLICT OF INTEREST

There is no conflict of interest declared in this article.

AUTHOR CONTRIBUTIONS

CJS, MJW and CLP conceived and designed the investigation. CJS, DHW, QEP and REC performed field and/or laboratory work. CJS, MJW and CLP analysed the data. DHW, QEP and REC contributed materials and/or analysis tools. CJS, MJW, CLP and DHW wrote the paper.

DATA AVAILABILITY STATEMENT

The data set that support the findings of this study are available from the corresponding author upon reasonable request.

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Additional supporting information may be found online in the Supporting Information section.

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**Additional supporting information**